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Dispersal evolution in a community context

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Dispersal evolution in a community context

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Abstract

Dispersal evolution in a community context

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Ecologists have long been interested in the consequences of dispersal for species interactions, trait evolution, and community coexistence. Less is known, however, about the impact of community structure or species interactions on the evolution of dispersal. In this report, I highlight recent research that has addressed this question and discuss how species interactions such as predation and parasitism affect dispersal evolution. Some noteworthy results include the selection on greater host dispersal as parasite search efficiency increases; the reversal on selection for dispersal in host individuals when a third trophic level is considered; novel mechanisms such as maternal provisioning that mediate the trade-off between competition and dispersal in plants. I also discuss how predictions for the evolution of dispersal change when multiple species are considered simultaneously. In a world where habitat fragmentation and climate change are increasing the pressure on species to move towards more favorable habitats, a better understanding of how dispersal is likely to evolve will help us predict range shifts and the future of communities in a more precise manner.

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Introduction

Dispersal can be defined as the movement of individuals or propagules from one habitat to another, from the site of birth to the site of reproduction (natal dispersal) or between successive sites of reproduction (breeding dispersal) in a manner that affects gene flow between populations across space (Ronce 2007; Matthysen 2012). Dispersal is an important process in ecology and its consequences can be seen at different biological levels.

At the individual level, dispersing to new habitats can improve chances of survival and reproduction by evading unfavourable conditions. Theoretical work indicates that mechanisms such as kin competition and inbreeding, can increase the probability of dispersal (Gandon 1999; Gandon and Michalakis 1999; Kiesecker and Blaustein 1999; Heino and Hanski 2001; Ronce 2001, 2007; Leturque and Rousset 2002; Jansen and Vitalis 2007). Similar effects have been found in models that consider crowding and density-dependent competition (Amarasekare 1998; Amarasekare and Nisbet 2001; Kisdi 2002; Perrin and Mazalov 2017), with support from empirical studies (Livingston et al. 2012; Fronhofer et al. 2015; De Bona et al. 2019). Models also predict that the presence of predators increases dispersal in populations (Taylor 1990; Kuang and Takeuchi 1994; Neubert et al. 1995). Selection for dispersal due to predation has been demonstrated in studies of natural and experimental populations (Günther 1992; Forrester 1994; Cochran-Stafira and Von Ende 1998). Similarly, studies have shown that dispersal can be selected for in models that consider the effect of parasites or pathogens on host populations (Dwyer and Elkinton 1992; Thrall and Burton 1997; Comins et al. 2002).

At the population level, dispersal is predicted to influence the gene flow between populations, affecting the persistence of metapopulations across landscapes (Hanski and

Gilpin 1991; Hanski 1998; Ilkka Hanski 1999; Hanski et al. 2004). Empirical evidence for the effect of dispersal on gene flow can be seen in studies of insect metapopulations (Loxdale et al. 2011). Dispersal is also vital in expanding the ranges of populations, as predicted by theoretical studies (Kirkpatrick and Barton 1997), and seen in empirical work (Holt 2003; Hughes et al. 2003; Duckworth and Badyaev 2007; Berg et al. 2010; Burton et al. 2010).

At the community and metacommunity level, dispersal has been theorized to affect community dynamics and biodiversity at local as well as regional scales (Leibold et al. 2004; Urban et al. 2008; Massol et al. 2011). Evidence for this has come from mesocosm experiments such as the study of the effect of processes at different spatial scales on local and metacommunity richness conducted by Cadotte (2006). In this study, the author used metacommunities of interconnected aquatic microbial communities and varied the level of dispersal between communities as well as the initial community composition. He discovered that global dispersal or no dispersal reduced local species richness, while metacommunity-level species richness was enhanced by initial community structure. The study also revealed the complex relationship between dispersal and variation in initial community composition.

Dispersal is also an important process in rescuing communities from adverse conditions such as environmental toxins (Low-Décarie et al. 2015; Malcom et al. 2015) or unfavourable climatic conditions (Kardol et al. 2011; Tesson and Edelaar 2013).

The impact of dispersal on species interactions and in the coexistence of species has become increasingly apparent recently (Urban et al. 2008; Rojas-Echenique and Allesina 2011; Vasseur et al. 2011; Norberg et al. 2012; Mittelbach and Schemske 2015). Community ecologists have highlighted the important role of regional processes in structuring biodiversity across spatial scales (Kneitel and Miller 2003; Kneitel and Chase

2004; Márquez and Kolasa 2013). In a meta-analysis, Cottonie (2005) highlighted the varying degrees to which spatial and environmental processes play a role in structuring communities. He showed that spatial scale accounted for a part of the variation in community composition detected across metacommunity structures. The analysis revealed that neutral dispersal processes accounted for more than 37% of the variation found in the metacommunities studied. In another example, Venail et al. (2008) showed using experimental metacommunities of the bacterium *Pseudomonas fluorescens* that regional diversity and productivity are linked to intermediate rates of dispersal. Their study also demonstrated that intermediate levels of dispersal increase regional diversity by increasing niche differentiation between genotypes, thus allowing coexistence of competing individuals over a more heterogeneous landscape.

However, we have little knowledge about how dispersal is in turn affected by species interactions. Dispersal evolution can be affected by several ecological and demographic factors. Classical studies show the importance of spatio-temporal habitat variation across a landscape in increasing individuals' propensity to disperse (Hamilton and May 1977; Comins et al. 1980; Bonte et al. 2010). These factors are weighed against the risk and costs associated with dispersal to give rise to optimal strategies (Dieckmann et al. 1999; Ronce et al. 2000; Ronce and Kirkpatrick 2001; Ronce 2007). Species interactions offer another level of complexity, adding to the spatio-temporal variation of populations, and modifying outcomes based on the species compositions of communities. For example, Chaianunporn and Hovestadt (2012a) showed that dispersal traits evolved differently in two-species metacommunities than four-species metacommunities comprising of hosts and parasitoids.

With greater insights from community ecology, there has been a in focus towards understanding evolution in community contexts (Thibodeau et al. 2015; Weber et al. 2017;

terHorst et al. 2018). Theoretical synthesis predicts that studying more than a single pair of interacting species at a time can alter the course of trait evolution both directly and through indirect or diffuse processes (terHorst et al. 2018). For example, in a study of protozoan communities living inside carnivorous pitcher plants, Miller et al. (2014) found that competitive interactions between species changed in a frequency-dependent manner, with initially competitive species becoming weaker over time and competitively weaker species gaining competitive ability over time. This is counterintuitive to the results one would expect when considering pairwise competitive interactions. The presence of additional species can also have indirect effects on selection for traits in pairwise interactions. For example, Gómez (2003) found that flower number in *Erysimum mediohispanicum* was selected for in the presence of pollinators. However, this effect was significantly reduced when ungulate herbivores were also present. The effect of interacting communities on the evolution of dispersal is still unclear, and must be better understood.

In this review, I delve into how the effect of species interactions on dispersal evolution has been addressed recently, and present the patterns of dispersal evolution that emerge in a host of different communities. I discuss how different dispersal traits such as the rate of dispersal and average distance travelled respond to trophic interactions such as competition, mutualisms, and antagonistic (such as host-parasite and predator-prey) interactions. The nature of interactions and the composition of the community can affect the evolutionary trajectory of dispersal traits in counter-intuitive ways. I further highlight important focus areas for future research that will help to promote our understanding of the evolution of dispersal at a broader level.

With an increase in habitat fragmentation and climate change, there has been an effort to understand the consequences of such changes for the evolution of dispersal (Thomas 2000; Schtickzelle et al. 2006; Schloss et al. 2012). The combined effects of

change in environment, along with biotic interactions are necessary to gain a deeper understanding of how dispersal will evolve in the future. It is important to understand how species interactions may be affected by changes to the community landscape. With many species moving towards the poles, and towards higher altitudes, knowledge about the ways in which dispersal may evolve in the future will also help us predict the future ranges of species, the impact that changes to interactions will have on these shifts, and what the consequences may be for coexistence and biodiversity.

The evolution of dispersal during invasions and range expansions

Having an understanding of the dynamics of invasions is essential to predict the consequences that invasive species have for the resident species in a given habitat, as well as the environment being invaded (Mack et al. 2000; Suarez and Tsutsui 2008; Ehrenfeld 2010). The process of dispersal has been at the heart of invasion events, accounting for a species' ability to successfully invade and establish in a given habitat (Panov et al. 2004; reviewed in Wilson et al. 2009). With environments changing rapidly in response to human activity and climate change, there is a push for a deeper understanding of the causes and consequences of invasion events. The leading edge of invasions, or range expansions, is often subject to a number of selective forces that can impact species' dispersive traits (Travis and Dytham 2002; Brown et al. 2014).

Some research suggests that the fastest and fittest individuals are often found at the range edge. This spatial sorting of dispersal traits is what is sometimes called the Olympic Village effect (Phillips et al. 2008; reviewed in Chuang and Peterson 2016). As these individuals reproduce, their offspring are selected to be fast and therefore, there is selection for increased dispersal at the range edge. This form of spatial selection is thought to segregate the slower individuals of the population, that are adapted to the higher densities of a core population, and the faster individuals to the edge (Shine et al. 2011). Individuals at the edge tend to experience lower intraspecific competition because the population sizes at the edge are smaller. This leads to an increased intrinsic population growth rate which provides further advantage to the frontier group (Phillips et al. 2008, 2010; Shine et al. 2011).

Models predict that spatial sorting in such populations leads to assortative mating among faster individuals found at the edge versus individuals at the core (Shine et al. 2011;

Perkins et al. 2013). Empirical evidence for this prediction shows there is a strong role of assortative mating in selecting for increased dispersal (Phillips et al. 2008, 2010; Léotard et al. 2009; Burton et al. 2010; Lombaert et al. 2014; Ochocki and Miller 2017). Ochocki and Miller (2017) demonstrated this by using mesocosms of bean beetles and disrupting the spatial sorting within populations. They showed that undisturbed populations had a greater dispersal speed and distance after just 10 generations. Surprisingly, the populations with spatial sorting showed a variance in dispersal distances that was 41.4 times higher than populations without spatial sorting. The study did not however see a difference in reproductive rates between the two treatments.

Spatial sorting appears to highlight evolutionary processes that are specific to invading populations. Some studies show that life-history traits trade off in unique ways in invading populations in conjunction with spatial sorting. Hudson et al. (2015) found that highly dispersive cane toads at the invasion front in Australia showed reduced reproductive rates when compared to less dispersive toads present in the core population. Trade-offs may also be more complicated when more variables are considered. A study by Burton et al. considered a model with trade-offs between dispersal traits, reproductive rates, and competitive ability in individuals during range expansion (Burton et al. 2010). In contrast to the results of Hudson et al., the model suggests that both dispersal and reproductive rates increase at the population edges. This prediction is in line with the hypothesis that lower competitive pressure at the edges creates a reproductive advantage for the frontier individuals (Phillips et al 2008). On the other hand, Travis and Dytham developed a model predicting that selection on dispersal is sensitive to the population density. The study suggested that Allee effects and low population sizes can reduce the selection on increased dispersal, as well as reduce the chance of survival of the species in the invaded habitat (Travis and Dytham 2002).

Burton et al. (2010) further found that differences between range and core individuals could be higher in dispersal traits than in reproductive rates. This suggests that the selective pressure on dispersal is higher and potentially more important to the success of an invasion or expansion event than increased reproduction at the range edge. In addition, increased competition from other species tended to weaken selection on dispersal, and greatly slow down expansions.

One of the more recent findings in studies of invasions is that dispersal traits may attenuate once expansion or invasion is complete and the population has established itself in a new environment. Once again, this phenomenon appears linked with life-history trade-offs. For example, studies on blue birds provide evidence to show that the birds that are less dispersive invest more in parental care, and this is selected for once populations are established, thereby reducing the overall dispersal levels in populations (Duckworth and Badyaev 2007). Sisson et al. (2013) also demonstrated a striking difference between invasion front individuals and post-colonization individuals in their dispersal abilities. Their study showed that invasive cane toads showed higher directionality and spent longer amounts of time dispersing everyday than post-invasion toads. Another observation obtained from their study was that the overall mean dispersal of the population was influenced by the spatial sorting taking place in expanding populations. As slower, less dispersive individuals arrive at a new environment, they reduce the mean dispersal of the overall population.

In some other cases, attenuation of dispersal traits has been attributed to a density cline among the traits (Shine et al. 2011; Perkins et al. 2016). Perkins et al. modelled both the effect of life-history trade-offs as well as the effect of population density on dispersal traits. They found that different situations are more affected by either process. However, the effect of trait trade-offs is exacerbated at higher densities. This study is noteworthy as

they also suggest what empirical patterns such processes might result in, providing insight into the kind of studies that may be useful in furthering our knowledge of such phenomena (Perkins et al. 2016).

Along with increased dispersal rate and distance, rapid adaptive evolution in novel environments has been found to play an essential role in successful invasions and range expansions. Adaptation can increase population growth rates and thereby increase chances of establishment (Melbourne et al. 2017). However, other studies show that adaptation can also decrease the growth rate as the population grows and competition for resources increases. This decrease in growth rate is linked to the increase in population size, which increases the intraspecific competition experienced by individuals for space and resources. At this stage, selection against growth rate enhances the survival of the overall population by stabilizing the population size (Hallatschek et al. 2007; Karlsson and Johansson 2008; Peischl et al. 2013, 2015; Altermatt et al. 2015).

Empirical evidence for the importance of adaptive evolution in shaping expansions is seen in studies such as the one conducted by Szűcs et al (2017). This study partitioned the effect of spatial evolution and adaptive evolution in a mesocosm expansion experiment comprising red flour beetles. By allowing or preventing the beetles to adapt to their new environments, the group showed that in just six generations, populations that were allowed to evolve grew three times bigger and spread 46% farther than populations that were prevented from evolving (Szűcs et al. 2017). In this case, however, spatial evolution contributed less than adaptive evolution, suggesting that it would be worthwhile to identify circumstances under which either process might contribute more to increased dispersal and successful establishment.

Competition and its impact on dispersal evolution

It has long been established that competition, both intraspecific and interspecific, can influence the optimal dispersal behaviour of organisms. The trade-off between competition and colonization has been well studied, showing that species with lower competitive abilities evolve higher dispersal to be able to establish in habitats where competition is low (Hamilton and May 1977; Calcagno et al. 2006; Cadotte 2007; Skarpaas et al. 2011; Pillai and Guichard 2012; Loeuille and Leibold 2014; Yu et al. 2014).

Species compete for space and resources, and both these mechanisms can result in the evolution of dispersal strategies. The number of resources for which species compete can influence the way in which dispersal evolves. One model suggested that species can minimize competitive pressure by adapting to specialize on individual resources, or by dispersing to empty habitats (Cenzer and M'Gonigle 2019). Such a landscape, with multiple resources that have different patterns of spatial autocorrelation, can support different dispersal strategies. In this model, the degree to which resource specialization and dispersal are linked determines the extent to which dispersal can be structured by resource competition (Cenzer and M'Gonigle 2019).

The mechanisms by which trade-offs between competition and dispersal occur can vary. In a study of annual plants in California, Germain et al. (2019) found that a trade-off between competition for resources and dispersal resulted in differential maternal provisioning of nutrients for seed mass. Seed mass is a trait that contributes to the dispersal ability of seeds. In general, it is thought that smaller seeds are better dispersers, while larger seeds are better at stress tolerance and survive for longer durations in the seed bank (Larios and Venable 2015). However, seed size is usually under high selection pressure and shows low variability as well has heritability (Mousseau and Roff 1987; Charmantier and Garant

2005; Visscher et al. 2008; as seen in Larios and Venable 2015). Using the annual winter plant, *Dithyrea californica*, Larios and Venable found evidence that plants produce smaller, more dispersive seeds when neighbourhood densities are high and that seed size was negatively correlated with dispersal distance. However, they found that seed size showed low heritability, supporting the above hypothesis. They found seed size to be largely dependent on maternal effects and environmental plasticity. The direct effect of the mother's seed size on the offspring seed size was only marginally significant and only in one of two study populations (Larios and Venable 2015). The maternal seed size was seen to have indirect effects on offspring seed size through plant mass.

The effect of neighbourhood density may be less straightforward, as Germain et al. (2019) found to be the case. The identity of the competitor affects the outcome of the competition. For example, in their study plots, they found that seed mass of *Salvia columbariae* decreased more as the relative frequency of its competitor *S. viridis* decreased. On the other hand, *S. columbariae* showed no significant changes to seed mass in the presence of *Collinsia heterophylla*. Competitive asymmetries played a role in how significant the response was in seed mass. The study also points out that concluding that species are competitively equivalent on the basis that they do not produce seeds in a frequency-dependent manner (Harpole and Suding 2007; Siepielski et al. 2010, as seen in Germain et al. 2019), may not always be valid. A frequency-dependent response in seed mass was not always accompanied by a change in seed numbers, suggesting that future research would benefit from considering seed mass as an indicator of competition and dispersal, in addition to seed number.

Different species respond differently to the presence of competitors (both intra- and interspecific). While some species respond by increasing seed mass, others adapt to the

increased pressure by decreasing seed mass and thereby increasing dispersal ability (Germain et al. 2019).

The addition of more trophic levels, leads to dispersal dynamics that are quite different from expectations outlined for systems with just one trophic level. The indirect effects imposed by other species in a food web are becoming more relevant to our understanding of community ecology (terHorst et al. 2018). In the context of dispersal, the effects of environmental variation on a species' resource and predator, can indirectly select for or against different dispersal strategies. Spatial variation in resource productivity and predator colonization ability can give rise to monomorphic dispersal strategies of mobile or sedentary individuals, and in some cases, could give rise to dispersal polymorphisms (Amarasekare 2016). Laroche et al. modelled how competition and metacommunity dynamics across a landscape create a feedback between dispersal strategies and landscape biodiversity (Laroche et al. 2016). Their model showed a distinct difference in dispersal evolution and the resulting biodiversity when they considered a competition-dispersal trade-off in metacommunities with varying carrying capacities across the landscape. They found spatial aggregation of dispersal traits around either a single ESS strategy or around distinct strategies (evolutionary branching or EB scenarios) when dispersal is limited and communities are not homogeneous. In EB scenarios, they found that individuals from larger communities presented lower dispersal and vice versa. They also found that when communities show branching in dispersal strategies, they tend to have higher alpha and beta diversities when compared to neutral metacommunities. They highlight the important relationship between community carrying capacities and dispersal in metacommunities (Laroche et al. 2016), as has also been noted by other studies (Jansen and Vitalis 2007). This relationship should be kept in mind when conducting further studies on the eco-evolutionary feedback between dispersal and metacommunity interactions.

Antagonistic interactions and their effect on dispersal

Predator-prey interactions are known to cause cycles or oscillations in communities, creating spatio-temporal variation in both predator and prey populations (Taylor 1990; Fussmann et al. 2007). The presence of spatio-temporal variation induces evolution of dispersal traits (Hamilton and May 1977; De Bona et al. 2019), and this is seen in predator-prey systems as well. Predators increase the chance of local extinctions which also increase the probability of dispersal (Holt 1984; McPeek et al. 1992; Hochberg and Ives 1999; D and Michael 2009; Poisot et al. 2014).

While the presence of predators has been shown to induce dispersal among prey, Hauzy et al. discovered that environmental cues of the predator's presence were sufficient to induce dispersal as well (Hauzy et al. 2007). Both predator and prey in their experiment showed interspecific density dependent dispersal- the predator, *Dileptus* sp. Showed increased dispersal when prey densities were low and the prey species, *Tetrahymena pyriformis* showed increased dispersal when predator densities were high. The prey species also showed higher dispersal when they encountered filtered medium that had previously contained the predator species indicating the importance of environmental and visual cues in mediating dispersal. Predator cues are also found to induce dispersal in other species. For example, some studies found that aphids produce winged morphs when they encounter predator cues (Poethke et al. 2010). In natural streams, researchers found that *Baetis thermicus* nymphs showed increased drift dispersal in the presence of visual, chemical, and hydrodynamic cues indicating the presence of benthic foraging fish (Miyasaka and Nakano 2001). Dispersal induced by the presence of predators or their cues, changes in a condition-dependent manner, which can only be observed when the whole community is studied. Studies now show that predicting movement or dispersal in metacommunities requires

knowledge of the strength and nature of inter- and intraspecific interactions (Poethke et al. 2010; Fronhofer et al. 2015).

Dispersal in predator-prey systems has strong implications for the persistence of the metacommunity at large. It can create or disrupt synchrony between local populations, thereby increasing or decreasing the chances of regional extinction respectively (Vasseur and Fox 2009; Fox et al. 2011; Mountain et al. 2012; Scranton and Vasseur 2016).

Similar to predator-prey systems, host-parasite/pathogen systems also induce cycles, and increase the probability of dispersal in both the host species and the parasite (Chaianunporn and Hovestadt 2012*a*; Kubisch et al. 2014). Studies have found the one important factor in structuring host-parasite dynamics is the search efficiency of the parasite. Research demonstrates that as search efficiency increases, host-parasite systems begin to closely resemble predator-prey dynamics in their cycles (Green 2009; Chaianunporn and Hovestadt 2012*a*, 2015, 2019).

Spatial heterogeneity has been shown, both theoretically and empirically, to select against dispersal (Hamilton and May 1977; Comins et al. 1980; Fussmann et al. 2007), while antagonistic interactions promote dispersal. Chaianunporn and Hovestadt looked at how these two opposing forces change dispersal when they act together in a host-parasitoid system (Chaianunporn and Hovestadt 2012*b*). The study found that heterogeneous habitats do continue to lower dispersal, but the magnitude of this effect is mediated by the strength of a trade-off between dispersal and fertility. Antagonistic interactions were once again shown to depend heavily on search efficiency. High search efficiencies in the presence of a strong life-history trade-off, however, selected against dispersal because the trade-offs created large fluctuations in host population size, increasing the risk involved in parasitoid dispersal (Chaianunporn and Hovestadt 2012*b*).

The relationship between host and parasite is also affected by the presence of other species and different trophic levels. Chaianunporn and Hovestadt extensively modelled host-parasitoid relationships and found that parasitoids generally evolve higher levels of dispersal than their hosts since dispersing into empty patches that contain no hosts would be costly and detrimental to them (Chaianunporn and Hovestadt 2012*a*). When a third trophic level- a hyperparasitoid is introduced to the system, the parasitoids consistently develop higher dispersal than the hosts because they are now evolving to escape parasitism themselves. The hyperparasitoid evolves the highest dispersal probability. They increase the stability of the host population by reducing the parasitoid load. This brings about interesting consequences for the host, because most patches become uniform in host density, reducing the advantage presented by dispersal in hosts (Chaianunporn and Hovestadt 2019). Empirical evidence for such a system and dispersal evolution of this kind was found by Nair et al. in a study of the Glanville fritillary butterfly and its parasitoid wasp, *Hyposoter horticola* (Nair et al. 2016).

A better understanding of the evolution of dispersal in pathogens will also help us address and prevent the rapid spread of diseases. Models show that dispersal may evolve in a number of ways depending on the stage of the infection in the population, and the strength of virulence. While the trade-off between virulence and transmission is well studied (Bull 1994; Ebert and Bull 2003), less is known about how the different stages of infection affect dispersal. Iritani and Iwasa Modelled disease dynamics to show that either infected or susceptible hosts can evolve to disperse more depending on the post-dispersal dynamics of the disease (Iritani and Iwasa 2014). When virulence of the pathogen is high and the transmission rate is high, susceptible individuals benefit from dispersing more. However, when virulence is low and the parasite load is low, dispersal is biased towards infected individuals. Low virulence among infected individuals also results in susceptible,

healthy individuals dispersing more. The bias in dispersal is mediated by relative costs of dispersal and the auto-correlation of disease states before and after dispersing (Iritani 2015).

Conclusion

The impact of species interactions on dispersal evolution is extensive and diverse. Some effects of species interactions are specific to the type of interaction, such as the role of search efficiency in antagonistic interactions, or the effect of seed provisioning in competitive systems. However, variables such as spatial heterogeneity, carrying capacities, etc., affect all community-level interactions. The combined effects of such common characteristics along with species interactions changes the trajectory of dispersal evolution in counterintuitive ways that must be investigated further.

Several studies have looked at how dispersal changes in a single generation in response to species interactions. How much of these changes are carried forward to future generations still remains unclear and is an avenue that must be investigated. Another important factor to be considered is the role of plasticity in condition-dependent dispersal. For example, in the case of predator systems, many prey species only dispersed when presented with the cues of the predator. It is unclear whether such dispersal is heritable or a plastic response to the environment. Similarly, the release of dispersal traits from strong selection following invasions also suggests that dispersal may evolve as a plastic trait in response to the environment. It would be worthwhile to investigate the role of plasticity in dispersal as a plastic trait, and to understand the different mechanisms through which condition-dependent dispersal evolves. Such studies will help us understand the long-term effects of the strength and nature of selection in more depth.

The consideration of multi-species interactions in models (such as tri-trophic host-parasitoid or resource-consumer systems) has demonstrated that dispersal can evolve in counterintuitive ways. As seen in studies by Chaianunporn and Hovestadt (2012a, 2015, 2019), or Amarasekare (2016), the direction of selection on dispersal traits may reverse

when additional species are considered. Some efforts are being made to understand this reversal in selection from an empirical stand point. However, a concerted effort is required, backed by models that provide predictions about the patterns in population dynamics that such combined interactions may cause (Duputie and Massol 2013; Altermatt et al. 2015)

As climate change and habitat destruction become more and more prevalent, efforts to understand the evolution of dispersal and its implications for species coexistence are vital. It would be beneficial to keep in mind the impact of such interactions on dispersal as efforts are made to contain the impact of human made climate change and in conservation efforts.

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